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Notes on the sub-social behaviour of adult mayflies (*Polymitarcys*) and on the lacunes in our knodledge of their life

Most mayflies have an adult longevity of a few weeks with a longer period for the total adult flight. They live scattered along the shcres oi lakes or rivers, and their imaginal life including reproduction is by no means different from that of other insects. Yet in a few species, for which the genus *Polymitarcys* (*Ephoron*) is an outstanding illustration, adult longevity is reduced to 2 to 3 hours, the period of imaginal flight in a given locality is reduced every year to about one week only. They hatch contemporaneously at the same hours of twilight or early darkness. Their life activity is very concentrated and reaches a high subsocial organisation during these few evening hours. The following notes concern observations made between the 10th to 16th September, 1951 on the great bridge over the Allier near Vichy. They want to point out the interesting subsocial behaviour of these swarms of *Polymitarcys virgo* Ol., and also to stimulate the study of the ecology and physiology of the adult life of these mayflies. Our knowledge regarding it has made almost no progress since the classical observations of Réaumur.

At varying hours, depending apparently upon the moon and upon air humidity, the hatching of *Polymitarcys* begins, usually shortly before 8 h p.m., at the surface of the river. They hatch rapidly, rising before the exuviae are fully cast off. Sometimes, on rainy evenings, nymphs crawl up by jerking movements to the bridge, where they hatch under heavy pulsations, which can be felt at their cephalic end.

To the best of our knowledge — yet we hesitate to be dogmatic on this point — only the males of *P. virgo* produce a subimago. Appendix A shows that considerable changes occur in the proportions of the extremities between the male subimago and imago, whilst we

never observed a moulting female and all females show uniformity in their measurements. In contrast to the Orthoptera and Rhynchota, — where the female doubles its weight after the last moult, adding thus a full stage of development, which the male does not do — these mayflies belong to the few insects, such as the Coccoidea, where the female has one stage of development less than the male. During these hours of hatching fishes are seen and heard jumping intensely out of the water to catch this preferred food. Observations are still wanting of the early behaviour of the hatched *Polymitarcys*: 1) if the males hatch before the females, 2) if copulation and swarming takes place immediately after hatching at a short distance above the water surface. Inspite of eargerly looking out we have never seen copulation later. Anyhow, in agreement with observations on other mayflies, copulation must be very rapid, which is astonishing, as the two penis have to be introduced into the two female gonopores.

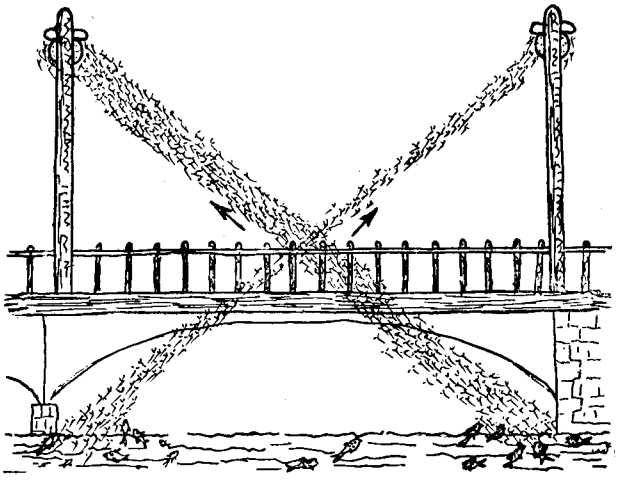

Fig. I.

The flight of *Polymitarcys* from the river to the lamps.

Very soon after hatching the flying mayflies, at least the females, are attracted by positive phototaxis to the electric lamps along the bridge and in its neighbourhood. For up to half an hour an unceasing stream of mayflies, following the few forerunners which preceded them, moves from the surface of the river, close to land, towards the lamps (Fig. I). The first forerunners are few and they flutter slowly around the light just as moths which are attracted to light (Fig. II, 1). Where

double lamps are present (at one m distance one from the other) both swarms remain strictly separated and no exchange of individuals was

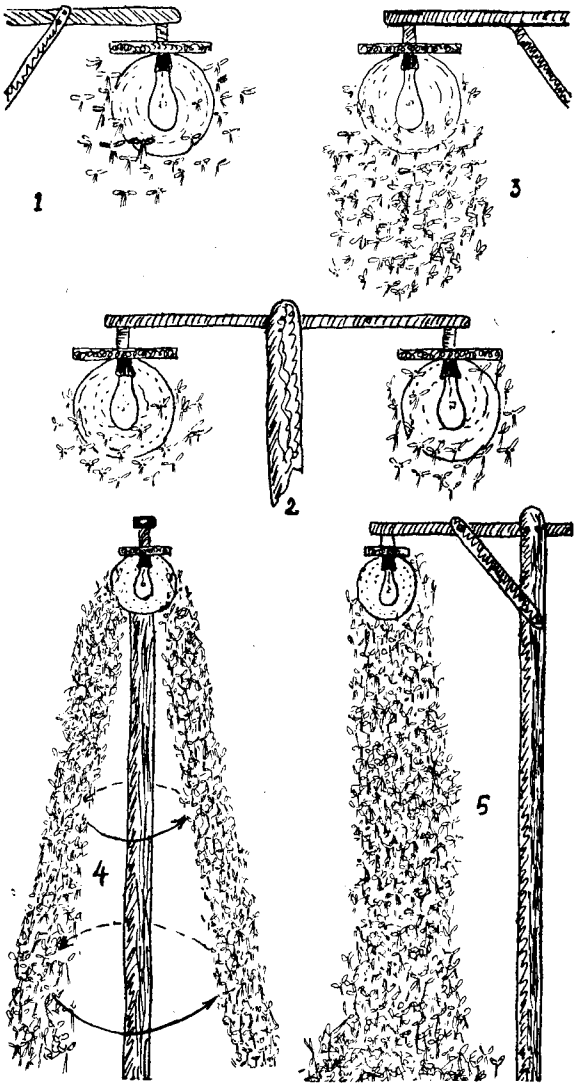

Fig. II.

Concentration, aggregation and sub-gregarisation of *Polymitarcys* on the light. Explanation in the text.

observed between both flocks (Fig. II, 2). When the swarm grows in size, the movements increase in speed and intensity, and heavy swar.

ming takes place underneath the lights (Fig. II, 3). The swarm continues to grow by new immigrants, always in a downward direction, so that it soon forms a massive « pole ». At this stage the intensity of swarming reaches its peak, its movements being twofold: Within the pole continuous heavy vertical movements take place, bringing the downmost individuals upwards, the uppermost ones down. Social behaviour has grown strong enough to overcome to some degree the phototaxis. At the same time the pole moves around the lamp in such a way that the upper part of the pole remains always attached to the light, and whilst it hinges on the light its distad parts perform complete circular movements around the lamp post (Fig. II, 4). After one

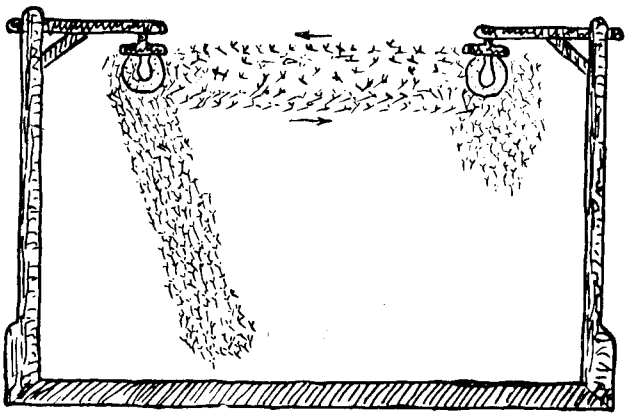

Fig. III.

Interference of two neighbouring lights on the swarming.

hour approximately of swarming the mayflies begin to die and to drop to the soil. The females by then have expulsed their two egg-heaps in two compact bodies, containing 500 to 800 eggs together, whilst the later arrivals still dance (Fig. II, 5).

The subsocial excitement has obviously the same importance as the synchronisation of stridulation on the large oviposition sites of locusts has for the stimulation of copulation and oviposition, namely to stimulate and to syinchronize the reproductive activity, speeding it up at the same time. On evenings, on which swarming is especially heavy, often contact is taken with the swarm of the lamp on the opposite side of the bridge, about 10 m distant, and a continuous circulation from one lamp to the other takes place (Fig. III). On the

11th September hatching began about 8 h p.m., and the whole phenomenon was over at 9.30 h. p. m.

Attraction to the light induces thus condensation of individuals, followed by active subsocial aggregation. The latter partially overcomes the photaxis, demonstrating again, that insects are no mere machines.

The egg pods when thrown into water drop to the botton, where they speedily dissolve into the isolated eggs.

One point in the physiology of adult *Polymitarcys* has not yet found sufficient attention. The integument (including that of the subimagos) is so soft, that the individuals are unable to move about by their legs. The intensive flight movements are made possible because the adults replace the normal support given to the muscles by the integument by another support given by the inflated intestines, a kind of inner skeleton. Long flights are impossible for these soft-skinned mayflies, whilst in the longer living species the integument hardens as in other insects.

In the heaps of dead mayflies the proportion was 90 females to 10 males.

The many outstanding problemes during the short adult lifespan of *Polymitarcys* can only be solved by organised observation, as one individual is definitely unable to observe all phenomena. One group must concentrate upon the observation of hatching and the behaviour of the just hatched individuals of both sexes at low altitudes above the water. The exact date and hour (starting from 6 h p.m.) of the begin of hatching and swarming of the mayflies should be studied for ten years with regard to the influence of temperature, light, humidity, etc. upon the hatching. Also the intensity of the flights from year to year should be compared. Attention should be given to which part of the mayflies rêmains above the water without being attracted to light (males, females). The exact place where the moulting of the nymphs takes place, requires attention, as well as the behaviour of the male subimagos.

Another group of observers will concentrate upon the phenomena from the arrival of the forerunners on the light to the death of the last individuals.

Laboratory studies are simultaneously required: 1) to analyse the type of phototaxis of the females (tropo — or telo — taxis), if the male subimagos and adults show the same degree of phototaxis as do the females; 2) to breed in deep vessels clods of earth with the ma-

ture nymphs, following the precedence of Réaumur, to study if the males hatch earlier than the females, if a female moult takes place, when and where copulation occurs, the mechanism of the nymphal moult and the previous replacements of the nymphs.

Only by organised observation of this kind the outstanding problems of mayfly biology can be solved. And France, the classical country of the *Polymitarcys* — flights, is the obvious place for such organised observations.

APPENDIX — SOME MEASUREMENTS OF THE THREE ADULT FORMS OBSERVED
(10 individuals each in mm.)

Character	Female	Sub-imago of male	Male
Body-length	9.00 (8.8-13.1)	11.59 (10.6-12.5)	11.31 (8.8-13.1)
Antennal joint I	0.61 (0.5- 0.7)	0.60	0.60
Antennal joint II	0.74 (0.7- 0.8)	0.72 (0.7- 0.8)	0.66 (0.6- 0.8)
Antennal joint III	3.45 (3.3- 3.6)	4.50 (4.2- 4.8)	4.35 (4.2-48)
Cerci	10.75 (10.0-11.9)	14.53 (12.5-16.3)	23.06 (20.0-25.0)
Median cercal process	—	0.56 (0.5- 0.6)	0.56 (0.5- 0.6)
Fore-femur	1.06 (0.9- 1.3)	0.88 (0.8- 1.0)	1.06 (0.9- 1.3)
Fore-tibia	1.25 (1.0- 1.4)	1.12 (1.0-1.3)	4.03 (3.8- 4.4)
Fore-tarsus	0.70 (0.6- 0.8)	0.75	4.12 (3.8- 4.8)
Mid-femur	1.04 (0.8- 1.3)	0.88	0.70 (0.6- 0.8)
Mid-tibia	1.02 (0.8- 1.3)	1.0	0.72 (0.6- 0.9)
Mid-tarsus	0.59 (0.5- 0.8)	0.62 (0.5- 0.8)	0.5
Hind-femur	1.25 (1.1- 1.3)	1.12 (0.5- 1.3)	0.97 (0.8- 1.3)
Hind-tibia	1.18 (1.0- 1.6)	1.21 (1.1- 1.3)	1.07 (0.9- 1.3)
Hind-tarsus	0.74 (0.6- 0.9)	0.62	0.68 (0.6- 0.8)
Fore-wing	12.7 (11.9-13.7)	8.79 (8.7- 9.3)	9.44 (8.8-10.6)
Hind-wing	5.51 (5.5- 6.0)	4.13 (3.8- 5.0)	4.81 (3.8- 5.0)
Eye (length diameter)	0.58 (0.5- 0.6)	0.50	0.50
Interval between eyes	1.20 (1.1- 1.4)	1.00	1.03 (1.0- 1.1)